

Species Relationships in a Marine Gastropod-Trematode Ecological System

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Abstract. Individual snails (*Ilyanassa obsoleta*) on Cape Henlopen, Delaware, frequently are host to one or more trematode species. When different species occupy the same host, interactions might be expected. We investigated five species of parasites to determine whether their existence in different combinations would lead to altered within-host distributions or changed numbers of shed cercariae. Snails (32 samples, total = 379) were collected from June to August, in 1989, and microscopically examined. Parasite species and stages present in five sections through each snail were recorded. Before examination, 206 of these snails were held in individual chambers in the field. After two high tides (*ca.* 24 h), the chambers were checked for species and the numbers of cercariae shed. Overall, 22 trematode combinations in single hosts were observed. Analysis revealed that co-occurrence with other species had no significant effects on any trematode. Further, analyses of species richness of infecting assemblages over two distinct intervals failed to show that competition is important in determining assemblage richness. One pair of trematodes (*Himasthla quissetensis* and *Lepocreadium setiferoides*) has been reported not to co-occur. We observed co-occurrences, but so few that the apparent conflict between them could not be statistically demonstrated. We suggest that, in this system, parasites are adapted to the host only; they may interact, but they are not adapted to each other. Chances for a parasite to live free from other parasites seem too great for evolved (adapted) relationships to develop. The host, for similar reasons, is probably not adapted to the parasites.

Introduction

For one species to be adapted to another, they must interact in such a manner that one consistently exerts a selective pressure on the other. Species interactions may be thought of as a continuum from local to global. A local interaction (as used here) results in genetic changes in restricted parts of a gene pool (and may result in local ecotypes). On the other hand, if an interaction is global, one species can be a source of biotic selective pressure over the whole operating gene pool of another. Reciprocal genetic changes between species amount to coevolution (Futuyma and Slatkin, 1983). This paper considers the species interactions in a marine gastropod-trematode system. Because the host gastropod has a planktonic larva and the trematodes are dispersed by highly mobile definitive hosts, both local and global phenomena must be considered.

The interactions between hosts and parasites have been much discussed (see Moore, 1987 for an extensive review), and the levels at which such discussions may be focussed should be distinguished. In this work, two levels are necessary. The component community includes all parasite species using a particular host species (population). The infracommunity includes all the parasites in a single host (Esch *et al.*, 1990). An individual host, harboring a multispecies parasite assemblage, is a biological unit where parasite-parasite as well as host-parasite interactions can occur.

There are four basic patterns of *evolutionary* relationships that may be found in any host-parasite system (Fig. 1a–d). In scheme a, the parasites are adapted to the host (the minimal condition), whereas in scheme b, the host is also adapted to the parasites. Scheme c illustrates the case where the parasites are adapted to the host and to

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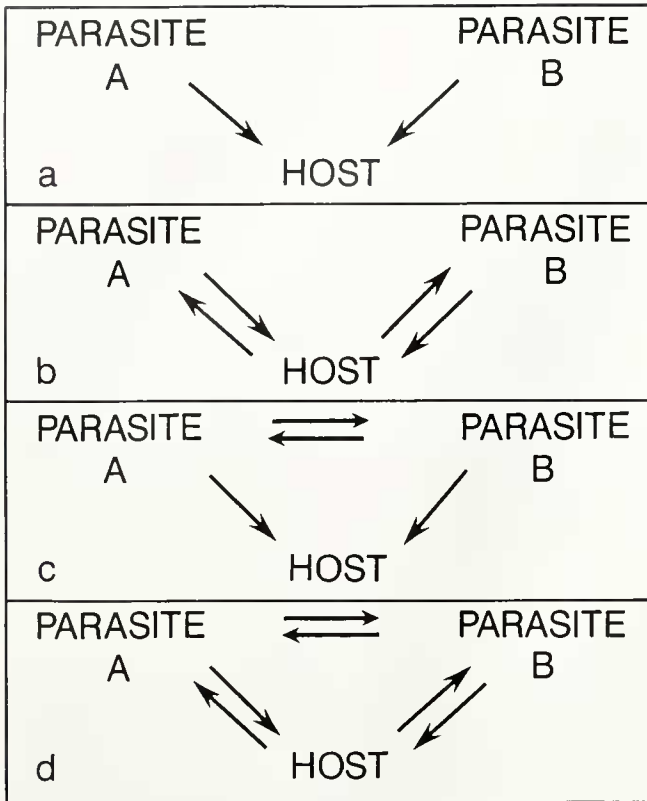


Figure 1. Four models of possible adaptive relationships among species in a snail-trematode system. Parasites A and B may coexist in a single host. An arrow from one participant to another indicates that the participant at the origin of the arrow has evolved adaptations to selection pressures coming from the other (i.e., "PARASITE A → PARASITE B" means A is adapted to B). One-way interactions between parasites (i.e., A adapts to B but not the reverse) are possible, but not figured.

each other. Scheme d shows the case where parasites are coevolved with the host and with each other. There should be evidence of an adaptive relationship between species before it is assumed to exist (Williams, 1966). In this work, we have tested for species interactions among trematodes inhabiting the same gastropod host. The goal is to gather evidence to support the elimination of one or more of the above schemes and thereby improve our understanding of host-parasite systems.

Studies of trematodes infecting gastropod populations have often revealed patterns of species co-occurrence that suggest interactions (see Rohde, 1981 for references). However, few workers have examined trematode assemblages in individual gastropods taken from their natural habitat, to determine whether fitness of certain members is consistently affected by co-occurrence with other members (see DeCoursey and Vernberg, 1974). This is largely because multiply-infected hosts are difficult to obtain in numbers for study. The prevalence of trematodes in the population of *Ilyanassa obsoleta* (Prosobranchia,

Neogastropoda) on Cape Henlopen, Delaware Bay is high, and a diversity of multiply-infected snails may be obtained (Curtis, 1985, 1987, 1990; Curtis and Hubbard, 1990). This allowed us to test for species interactions in a variety of trematode ensembles.

Of the nine trematode species in *Ilyanassa obsoleta* observed in Delaware, five are commonly observed in the Cape Henlopen population and figure in this study: *Himasthla quissetensis*, *Lepocreadium setiferoides*, *Zoogonus rubellus*, *Austrobilharzia variglandis*, and *Gynaecotyla adunca*. The snail is the first intermediate host. A variety of second intermediate hosts is used by these species. Various shorebirds serve as definitive hosts for *H. quissetensis*, *A. variglandis* and *G. adunca*, whereas fish species are used by *L. setiferoides* and *Z. rubellus* (see Stunkard, 1983 for life-cycles and taxonomic matters). Any direct species interactions among these parasites must occur in the snail, the only host they all have in common.

There is no indication that *Ilyanassa obsoleta* lose infections (Curtis and Hurd, 1983), so the ensembles observed in snails probably represent relatively longstanding (period unknown) assemblages. Enduring species assemblages, proximity in a natural habitat unit, and utilization of similar resources (Smyth and Halton, 1983), suggest that strong interspecific interactions might occur.

If competitive interactions are frequent within individual hosts whereby dominant species come to monopolize the host population through time, a pattern should emerge at the component community level. Early on, most snails should have single species infections; as time progresses species accumulate and there should be a preponderance of double and triple infections; and eventually there should be mostly single infections again, as the dominant species evict subordinates (Sousa, 1990). We searched for such a component community pattern among our snails at two time scales, through the summer and over several years.

To examine within-snail parasite interactions, we tested individual species to see whether existence in different assemblages had consequences in terms of (1) alterations of within-snail spatial distributions, (2) complete suppression of cercarial production, and (3) changes in numbers of cercariae released from hosts.

Materials and Methods

One sandbar (Fig. 2), located near the mouth of the Delaware Bay on Cape Henlopen (75° 06'W, 38° 47'N), was chosen as the source for snails. Certain species of trematodes affect the behavior, distribution and temporal occurrence of *Ilyanassa obsoleta* on sandbars (Curtis, 1987, 1990). To avoid over-representing snails harboring particular parasite ensembles, we randomly chose collection sites according to the angle and distance from a reference point at the peak of the sandbar (Fig. 2). Samples

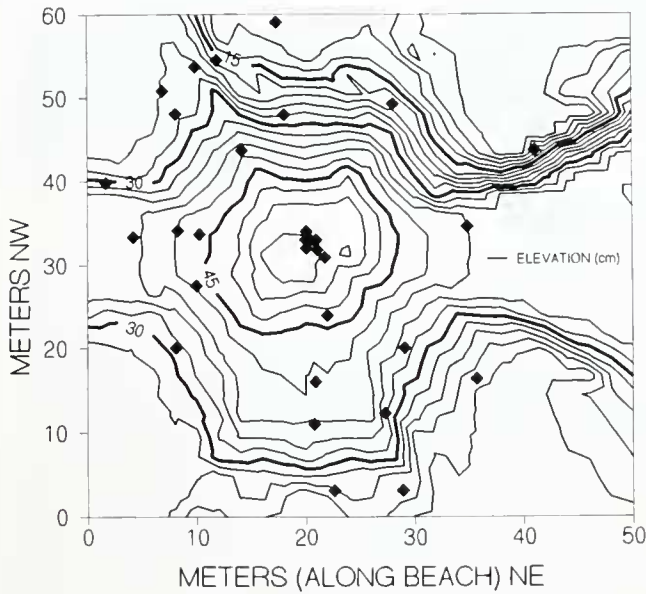


Figure 2. An elevational contour map of the 1989 sandbar on Cape Henlopen, Delaware where samples of *Ilyanassa obsoleta* were collected for this study. The 32 randomly selected sample sites are indicated by filled diamonds. The highest point on the map (the sandbar peak at center) is 56 cm above the lowest.

were taken between 16 June and 17 August 1989 on both day and night low tides. We wanted many multiply-infected snails in the samples, and the 379 snails obtained (Table 1) were purposely biased to include them. The snails came from an area where many multiples were likely to be found (e.g., Curtis, 1987), and large snails that were likely to be infected were chosen (Curtis and Hurd, 1983). Usually, two collections of 10 to 13 snails were collected and processed at a time. All the snails were dissected and 206 were also tested for cercarial release.

We were interested in revealing gross within-snail displacements of individual parasite species by other species or combinations of species. Such displacements would be required if dominant species gradually evicted subordinates from the snail. During dissection each snail was removed from its shell and examined in sections to determine how individual parasite species, and stages thereof, were distributed within. Heavily parasitized snails are virtual bags of trematodes; they retain no consistent morphological landmarks that are useable as standard points of reference. Consequently, each snail was pinned to a board and cut crosswise into five equal lengths with a razor blade. Section 1 was the most dorsal portion of the snail (the spire), and section 5 was the most ventral (head and foot). The razor was cleaned between cuts and scrupulous care was taken to prevent contamination of one section with material from another.

Sections were placed separately in small vials containing 5 ml filtered baywater. Each vial was vigorously shaken

50 times to release the contained trematode stages into the water. A small amount of the water was placed on a slide and examined with the aid of dissecting (32 \times) and compound (100 \times) microscopes. We took two samples from each vial. The species and stages of the trematodes were recorded for each section of each snail as follows: parental stages (rediae or sporocysts) and cercariae (PC); cercariae only (C); parental stage without mature cercariae (P); or absent (A). Observed cercariae may have been liberated from parental stages during the procedure, but this does not matter as we were only interested in whether formed (mature) cercariae were present. Trematodes were never found in section 5, and after the hundredth snail we stopped examining this section.

Table 1

Trematode infections in Ilyanassa obsoleta collected for this study from a sandbar area (Fig. 2) on Cape Henlopen, Delaware

Infecting species	n	Mean shell height (mm)	Range shell height (mm)
uninfected	18	21	17–25
singles			
Hq	74	24	20–27
Ls	25	24	20–27
Zr	29	22	20–26
Av	5	23	22–24
Ga	29	22	18–25
doubles			
HL	4	23	22–23
HZ	42	24	20–27
HG	10	23	21–25
LZ	8	24	20–28
LA	1	25	—
LG	32	23	20–26
ZA	1	24	—
ZG	24	23	20–27
AG	10	22	19–24
AD	1	23	—
GD	1	21	—
triples			
HZG	33	24	18–26
LZA	1	28	—
LZG	22	23	17–26
LAG	4	21	20–24
ZAG	5	23	23–25
Total =	379	Overall =	23
			17–28

For each infection, number collected (n), and mean and range of shell heights are given. Snails infected by a single species (singles) are represented by the genus and species initials of the trematode (Hq = *Himasthla quissetensis*, Ls = *Lepocreadium setiferoides*, Zr = *Zoogonus rubellus*, Av = *Austrotilharzia variglandis*, Ga = *Gynaecotyla adunca*). Double and triple infections are represented with the generic initials of the species involved (e.g., a snail infected with *H. quissetensis*, *Z. rubellus*, and *G. adunca* goes in the HZG category). *Diplostomum nassa* (D) occurred only in double infections. Shell height = siphonal canal to apex of shell (e.g., 21 = 20.5 to 21.4 mm).

The frequencies of parasite presence or absence in the snails were crosstabulated according to the following criteria: parasite assemblage (those species infecting the snail); snail section (1–4); and the stage of the parasite (sporocysts, rediae, cercariae). Contingency table analyses were employed to test for significant displacements of parasite stages within snails. For each parasite, we used log linear models (Sokal and Rohlf, 1981) to calculate the expected frequencies of occurrence of the stages (PC, P, C, or A) in various sections of hosts harboring various trematode ensembles. A saturated log linear model for this kind of analysis includes seven terms: Assemblage; Section; Stage; Assemblage \times Section; Assemblage \times Stage; Section \times Stage; and Assemblage \times Section \times Stage. The purpose of this analysis is to learn which of these terms are necessary to calculate a set of expected frequencies that do not deviate significantly from the observed frequencies. After unnecessary terms are eliminated, we are left with the accepted model. The accepted model is expressed in hierarchical form. For example, an Assemblage \times Section \times Stage hierarchical model would nest all seven terms of the full model; and an Assemblage, Section \times Stage model would nest all three one-way terms and the Section \times Stage two-way term.

If species interactions lead to spatial rearrangements within snails, a 3-way interaction term (*i.e.*, Assemblage \times Section \times Stage) would be necessary in the accepted model for any displaced species. For example, suppose species "a" were usually distributed throughout the snail from spire to mantle when it occurred alone, but in the presence of species "b" (*i.e.*, assemblage "ab"), "a" were consistently absent from the spire section. The three-way interaction term would be necessary in the accepted model because absence (A) of species "a" from Section 1 would be a consequence of Assemblage composition. That is, the presence of species "b" in Section 1 would change Stage entries for "a" in Section 1 to absent (A) from one of the present categories (PC, P, or C). Therefore, a table of expected frequencies that matched observed frequencies could not be calculated without the Assemblage \times Section \times Stage term in the accepted model.

We used cercarial release as a measure of fitness to learn whether parasites were affected by within-host interactions with other infecting species. We evaluated cercarial output from assemblages during one short period, and tested similar assemblages throughout the summer. (An alternative, more manipulation laden, approach would be to follow cercarial output from individual assemblages over a longer period of time.) Individual snails were confined in chambers in the natural environment for two high tides (*ca.* 24 h), and the water in which they had been immersed was examined for numbers and species of cercariae. We used 24-h periods to encompass any daily shedding patterns. The procedure is described in

more detail in Curtis and Hubbard (1990). We used a Kruskal–Wallis test (Hollander and Wolfe, 1973) to determine, for each species, whether the number of cercariae shed was significantly different when in various co-occurring assemblages of parasites. All statistical calculations were done with the software package, Number Cruncher Statistical System, 5 \times Series.

Results

A competition model (Sousa, 1990) suggests that trematodes might invade a snail population, accumulate in snails, compete, and eventually complete the process by having dominant trematodes evict subordinates. If true, then over the relevant time we should see infecting species richness start low (mostly single infections), increase (mostly doubles and triples), and then decrease again. We looked for such a pattern within two distinct intervals, over the summer (Table IIA), and over several years (Table IIB). We divided the sampling period into four two-week intervals; the fourth interval was extended to encompass the 25 snails collected on August 17. There were significant changes in richness from one period to the next, but the expected pattern was not seen. In particular, triple infections were quite abundant early in summer and were most abundant in the last sampling period. This would not have been observed if dominant trematodes had defeated subordinates in this period of time.

Using size-classes of snails (Table IIB), the interval can be extended from months to years. At the beginning of its third summer, a snail on Cape Henlopen is about 14–15 mm; by the end of that summer, it has grown to about 17–18 mm (Curtis and Hurd, 1983). This means that the smallest snails we collected (17 mm, Table I) were probably in their fourth summer. If 3 mm/summer is used as an estimate of growth for parasitized snails, then the < =22 group in Table IIB is 4–5 yr old; the 23–25 group is 5–6 yr old; and the 26–28 group is 6–7 yr old. The interval encompassed by Table IIB is about three years using this estimate. Parasitized snails may not grow this rapidly, and the interval is possibly longer. In this years-long interval (size-class range), there were significant changes in infecting species richness. Note (Table IIB) that single infections were more abundant than triple infections in the youngest snails, but that the proportion of triples increased among older snails. This is not the pattern predicted by the competition model.

Occurrence of stages of five trematodes in sections of *Ilyanassa obsoleta* harboring different assemblages is shown in Table III. Recall that section 1 was dorsal (spire) and section 4 ventral (mantle). In Table IV, models for all five species (except *Austrobilharzia variglandis*) require the one-way Assemblage term because of the widely different numbers of snails infected with each assemblage

Table II

Trematode infections in Hymanassa obsoleta examined during this work crosstabulated by number of infecting trematode species (richness), time of collection in summer 1989 (A), and size (age) of snail (B)

	Infecting Species Richness				n =
	% NI (n = 18)	% Singles (n = 162)	% Doubles (n = 134)	% Triples (n = 65)	
A. Time Collected					
16 Jun–29 Jun	0.9	39.8	44.3	15.0	113
30 Jun–13 Jul	15.0	38.7	40.0	6.3	80
14 Jul–27 Jul	1.1	50.0	30.7	18.2	88
28 Jul–17 Aug	4.1	42.9	25.5	27.5	98
B. Size Class (mm)					
< = 22	10.5	43.8	33.3	12.4	153
23–25	1.0	43.6	36.9	18.5	195
26–28	0.0	32.3	35.5	32.3	31

2-way contingency analyses:
 Time × richness, $\chi^2_{(3)} = 43.69$, $P < 0.001$
 Size × richness, $\chi^2_{(6)} = 25.16$, $P < 0.001$

Size class ranges are in terms of shell height as in Table I.

(see Table III). The frequencies for *Lepocreadium setiferoides* can be modeled by taking into account, beyond the Assemblage term, only the one-way Stage term because most of the stage entries are in the PC category. The rest of the models require the Section × Stage term because there was some specificity as to what sections were likely to harbor which stages. This is clearest for *Zoogonus rubellus* and *Gynaecotyla adunca*. Stages were often (clearly not always) absent (A) from sections 1 and 4. However, this was not significantly correlated with the assemblage of species infecting the snail. For none of the five species tabulated is an Assemblage × Section × Stage (three-way) interaction term necessary in its accepted hierarchical log linear model (Table IV). That is, co-occurring trematodes did not significantly affect the distribution of any of the five species tested. In most snails, parasite stages of all species present occurred throughout.

Parasite species interactions could lead to cercarial suppression in a section rather than species eviction. For example, if the presence of species “a” suppressed cercarial production by species “b”, the accepted log linear model for species “b” would have to include the Assemblage × Stage term. This would be necessary because, for species “b” in the presence of species “a”, the frequency of the PC category would decrease, while the frequency of the P category would increase as compared to other assemblages involving species “b”. Expected values that matched this shift in observed frequencies could not be predicted (modeled) without incorporating the influence of Assemblage on Stage. No species’ cercarial production was completely suppressed in this manner (Table IV, lack of Assemblage × Stage terms).

The question now becomes: given that cercariae were being produced, was the number released from snails changed as a function of assemblage composition? To answer this, we used data from cercarial release chambers. Prepatent infections (those with no cercariae present) were eliminated from this analysis because their prepatency was not caused by assemblage composition (Table IV, no Assemblage × Stage terms in the accepted models). Including prepatents would add meaningless variability. Absent cercariae are not germane to this analysis if they are not caused by the presence of other species. Table V describes statistically the cercarial output of each of the five species in various assemblages. The magnitude of variability should be noted.

Table VI presents the results of Kruskal–Wallis tests that were used to determine whether the assemblage composition significantly affected the numbers of cercariae released by particular (patent) assemblage members. The results show that although cercarial output (mean rank) did decrease for all species when additional species were present, there was not a significant depression of cercarial output for any one species.

Finally, because *Himasthla quissetensis* and *Lepocreadium setiferoides* have not previously been observed together, note that in Table V such a co-occurrence is listed, and that both species shed cercariae concurrently. Four snails contained both *H. quissetensis* and *L. setiferoides* (Table I). Based on observations of a few mature (often moribund) *H. quissetensis* rediae and cercariae among many *L. setiferoides* rediae and cercariae, it appeared that *L. setiferoides* was evicting *H. quissetensis* from the snails. There were not enough of these snails to

Table III

Spatial distributions of five trematode species (see Table I for parasite abbreviations) within singly- and multiply-infected *Ilyanassa obsoleta*. Observed frequencies of parasite occurrence (by stage*), in snail sections 1–4 (see text), are given for each species

Infecting trematodes	Species tabulated	Section															
		1 Stage				2 Stage				3 Stage				4 Stage			
		PC	C	P	A	PC	C	P	A	PC	C	P	A	PC	C	P	A
Hq (n = 74)	Hq	72	1	1	0	73	0	1	0	73	1	0	0	69	2	1	2
HZ (n = 42)	Hq	38	0	2	2	40	0	0	2	40	1	0	1	33	6	2	1
HG (n = 10)	Hq	6	0	3	1	10	0	0	0	9	0	0	1	8	0	1	1
HZG (n = 33)	Hq	30	0	2	1	33	0	0	0	32	0	1	0	27	2	0	4
Ls (n = 25)	Ls	25	0	0	0	25	0	0	0	24	1	0	0	22	3	0	0
LZ (n = 8)	Ls	8	0	0	0	8	0	0	0	8	0	0	0	7	1	0	0
LG (n = 32)	Ls	26	4	2	0	32	0	0	0	30	0	2	0	23	2	3	4
LZG (n = 22)	Ls	19	2	1	0	21	1	0	0	21	1	0	0	17	5	0	0
Zr (n = 29)	Zr	27	0	0	2	27	0	0	2	27	0	0	2	17	0	0	12
HZ	Zr	25	0	0	17	37	0	0	5	38	0	0	4	26	2	0	14
LZ	Zr	4	0	0	4	8	0	0	0	7	1	0	0	2	0	0	6
ZG (n = 24)	Zr	22	0	0	2	24	0	0	0	23	0	0	1	10	0	0	14
HZG	Zr	20	0	0	13	30	0	0	3	32	0	0	1	17	0	0	16
LZG	Zr	12	0	0	10	21	0	0	1	21	0	0	1	8	0	1	13
ZAG (n = 5)	Zr	3	0	0	2	4	0	0	1	5	0	0	0	0	0	0	5
Av (n = 5)	Av	4	1	0	0	5	0	0	0	4	0	0	1	2	0	0	3
AG (n = 10)	Av	7	0	0	3	10	0	0	0	10	0	0	0	2	0	0	8
ZAG (n = 5)	Av	3	0	0	2	5	0	0	0	1	0	0	4	0	0	0	5
Ga (n = 24)	Ga	25	0	0	4	28	0	0	1	26	0	0	3	16	1	0	12
HG	Ga	6	0	0	4	9	0	0	1	10	0	0	0	4	1	0	5
LG	Ga	23	1	1	7	29	0	1	2	29	1	0	2	16	2	0	14
ZG	Ga	20	0	0	4	22	0	0	2	24	0	0	0	15	0	0	9
AG	Ga	9	0	0	1	9	0	0	1	9	0	0	1	8	0	0	2
HZG	Ga	21	0	0	12	28	0	0	5	32	0	0	1	10	0	0	23
ZG	Ga	14	0	0	8	17	0	0	5	21	0	0	1	13	0	0	9
AG	Ga	4	1	0	0	5	0	0	0	5	0	0	0	4	0	0	1

* Stage abbreviations: PC = parental stage (*i.e.*, sporocysts or rediae) plus cercariae; P = parental stage only; C = cercariae only; and A = all stages absent.

Individual species occurred in the context of several different combinations of infecting species (*e.g.*, Hg occurred alone, in HZ and HG doubles, and in HZG triples). For each species, frequencies are tabulated for each context. The number (n) of snails infected by particular trematode assemblages is indicated. Assemblages found in fewer than four snails are not tabulated.

be included in the above log linear or Kruskal–Wallis analyses.

Discussion

Ilyanassa obsoleta is the only shared host in the life-cycles of these trematode species and is, therefore, the only place they might directly interact. They are tightly packed together in the snail, gather resources in similar ways, and are abundant on Cape Henlopen. Antagonistic interactions between trematode assemblage members have been noted by several investigators (*e.g.*, Lie *et al.*, 1965; Basch *et al.*, 1969; DeCoursey and Vernberg, 1974; Kuris, 1990; Sousa, 1990). On such grounds we anticipated that trematodes co-occurring in *I. obsoleta* would interact and most likely compete. A between-snail (component com-

munity) analysis indicated that competition within snails was not an important determinant of the number of trematodes infecting individual snails. Further, regarding within-snail phenomena, no effect of assemblage composition on any individual species could be discerned statistically. However, *Himasthla quissetensis* and *Lepocreadium setiferoides* were seen to co-occur in this study for the first time (Tables I, V), and this observation deserves special comment. By virtue of their rare co-occurrence, which eliminated the pair from our statistical analyses, these species apparently do interact negatively when they occur in the same snail.

Our sample of trematode assemblages from the Cape Henlopen sandflat naturally included only those species combinations that can coexist long enough to be observed by the methods used. These included most of the possible

Table IV

Results of loglinear analyses testing the influence of three factors (trematode Assemblage, snail Section, and parasite Stage) on the frequencies of within snail occurrence reported in Table I

Species analyzed	Hierarchical log-linear model accepted	χ^2	d.o.f.	$P = *$
Hq	Assemblage, Section × Stage	54.21	45	0.163
Ls	Assemblage, Stage	67.33	57	0.165
Zr	Assemblage, Section × Stage	63.25	90	0.985
Av	Section × Stage	25.79	32	0.773
Ga	Assemblage, Section × Stage	60.99	105	0.999

* An insignificant χ^2 ($P > 0.05$) without the three-way interaction term means that it is unnecessary; no significant displacement occurred.

If a trematode's stages (*i.e.*, sporocysts, rediae, cercariae) were displaced from one snail section to another by the presence of a co-occurring species or combination of species, the accepted model for that trematode would require the three-way interaction term (*i.e.*, Assemblage × Section × Stage) to calculate expected frequencies without significant deviation from the observed.

assemblages and virtually all that might have been expected to occur. Twenty, of the 32 possible for five species analyzed, were actually observed (Table I). Missing assemblages were the quintuple, the five quadruples, multiples involving the scarce *Austroilharzia variglandis*, and two triples involving *Himasthla quissetensis* and *Leporecardium setiferoides*.

A major concern is whether interparasite competitions occur that require considerable time for completion. In the early to middle phases of competition there may be no noticeable effect on any one species. We may have examined most assemblages at a time when coexistence is possible, and erroneously concluded that species do not interact. If such a time-course for competition is involved, how much time is necessary, and was our collection of parasite assemblages (in snails) biased by this? Two possibilities present themselves: competitions could play themselves out over the summer; or over several summers. There was no indication that trematodes assemble in snails, compete, and ultimately evict subordinate species in either the short or the long interval (Table II). To the contrary, species appear to collect in snails as a function of time. Note that older snails, and not either younger group, have the largest proportion of triple infections (Table IIB). Sousa (1990) looked for a hyperbolic relationship between snail size and infecting species richness and similarly did not find one.

Direct measurements of within-snail species dynamics also indicate no interactions among assemblage members. The occurrence of parasitic stages in different sections of variously infected snails is shown in Table III. No species

was excluded from sections of snails because of co-occurring species (lack of Assemblage × Section × Stage terms in Table IV). If one species (or combinations of species) leads to gradual eviction of another species from snails, this phenomenon should have been quite common. Neither was cercarial production (from existing parental stages) of any species shut down by co-occurring species (lack of Assemblage × Stage terms in Table IV). Also, there was no indication that cercarial output from hosts (an estimate of fitness) was influenced by co-occurring species. There was no statistically significant reduction of cercarial output of any species as a function of assemblage

Table V

Descriptive statistics associated with numbers of trematode cercariae released per host (*Ilyanassa obsoleta*) in 24 h in the field. Information is grouped by species of cercariae being tabulated (see Table I for species abbreviations)

Infecting trematodes	Cercariae tabulated	Mean #	S.D.	Max.	Med.	Min.
Hq (n = 42)	Hq	527	709	2739	225	0
HL (n = 1)	Hq	18	0	18	18	18
HZ (n = 23)	Hq	211	344	1428	90	0
HG (n = 4)	Hq	696	1135	2388	177	42
HZG (n = 22)	Hq	155	274	1233	60	0
Ls (n = 18)	Ls	319	590	2394	129	0
HL (n = 1)	Ls	567	0	567	567	567
LZ (n = 2)	Ls	130	185	261	131	0
LG (n = 10)	Ls	42	66	165	9	0
LZG (n = 15)	Ls	121	153	483	45	0
LAG (n = 2)	Ls	18	25	36	18	0
Zr (n = 12)	Zr	249	378	1095	15	0
HZ (n = 20)	Zr	68	199	882	1	0
LZ (n = 2)	Zr	0	0	0	0	0
ZA (n = 1)	Zr	1065	0	1065	1065	1065
ZG (n = 8)	Zr	61	67	189	42	0
HZG (n = 19)	Zr	47	73	210	6	0
LZG (n = 13)	Zr	79	138	474	21	0
ZAG (n = 2)	Zr	12	8	18	12	6
Av (n = 3)	Av	0	0	0	0	0
ZA (n = 1)	Av	0	0	0	0	0
AG (n = 5)	Av	9	16	36	0	0
LAG (n = 3)	Av	21	16	33	27	3
ZAG (n = 1)	Av	6	0	6	6	6
Ga (n = 14)	Ga	222	454	1398	0	0
HG (n = 3)	Ga	6	10	18	0	0
LG (n = 8)	Ga	74	168	483	0	0
ZG (n = 6)	Ga	0	0	0	0	0
AG (n = 5)	Ga	3	5	12	0	0
HZG (n = 17)	Ga	2	9	36	0	0
LZG (n = 13)	Ga	27	96	345	0	0
LAG (n = 4)	Ga	6	12	24	0	0
ZAG (n = 1)	Ga	18	0	18	18	18

Only infections that were patent for the species being tabulated are considered (n). For example, there were 33 HZG-infected snails (from Table I); 22 of these were patent for Hq; 19 for Zr; and 17 for Ga. A total of 206 snails were tested for cercarial release.

Table VI

Results of Kruskal-Wallis tests evaluating the null hypothesis for each trematode species (see Table I for species abbreviations), that the number of cercariae shed was unaffected by coexisting species

Effect of coexisting species on fitness of	Infecting species	Mean rank (# cercariae)	d.o.f.	Kruskal-Wallis H	P =
Hq	Hq (n = 42)	52.583	3	6.454	0.091
	HZ (n = 23)	41.957			
	HG (n = 4)	53.500			
	HZG (n = 22)	36.295			
Ls	Ls (n = 18)	23.972	2	3.186	0.203
	LG (n = 10)	15.850			
	LZG (n = 15)	23.733			
Zr	Zr (n = 12)	42.417	4	5.254	0.262
	HZ (n = 20)	29.575			
	ZG (n = 8)	42.563			
	HZG (n = 19)	33.763			
Av Ga	No test		6	8.075	0.233
	Ga (n = 14)	39.536			
	LG (n = 8)	39.688			
	ZG (n = 6)	26.500			
	AG (n = 5)	38.100			
	HZG (n = 17)	28.471			
LZG (n = 13)	33.537				
	LAG (n = 4)	34.375			

Prepatent infections and trematode assemblages observed fewer than four times were excluded.

composition (Table VI). There was much variation, even in single infections (Table V), suggesting that sources of variability other than co-occurring species control cercarial output.

DeCoursey and Vernberg (1974) studied assemblages of trematodes infecting *Ilyanassa obsoleta* in North and South Carolina. At the level of the component community, they noted that some species co-occur in multiple infections more or less often than would be expected based on the abundance of each in the system. They proposed that such patterns are produced by antagonisms or affinities among assemblage members. About 80 snails were dissected, with 30 of these being serially sectioned. The number of snails examined in each assemblage category is not reported. The authors noted "marked overlap in territory and habitat preferences," as we did in this study. Contrary to our conclusion (based on arbitrary snail sections) that the parasites are not displaced, they concluded that some species are displaced from preferred sites (specific snail organs) by other species. Even if small scale displacements (*i.e.*, from organ to organ within our arbitrary sections) do occur, they would have to result in reductions in cercarial output (fitness) to have evolutionary consequences. Cercarial output was not significantly

reduced (Table VI). We also note that, if the interest is in adaptation of one parasite to others (Fig. 1), then sectioning snails along snail organ boundaries confounds adaptation to other parasites with adaptation to the host.

In the laboratory, DeCoursey and Vernberg (1974) also counted the cercariae released from 10 infected snails. Three were infected with *Zoogonus lasius* (= *rubellus*) and five with *Lepocreadium setiferoides*. The remaining two were doubly infected with these same species. The numbers of cercariae released in the laboratory by each species of trematode were averaged and compared. When *Z. rubellus* and *L. setiferoides* occurred alone, they each released approximately 3500 cercariae in 24 h. When the species co-occurred, they released 901 and 1477, respectively. The authors concluded that *L. setiferoides* suppressed cercarial release by *Z. rubellus*. Data show that cercarial production of both species was lower when they co-occurred. In any case, the number of observations precludes meaningful statistical inference.

We are interested in eliminating inoperative models from the four presented in Figure 1. Williams' (1966) distinction between "functions" and "effects" seems useful here. Functions are biological characteristics that are direct products of natural selection (adaptations), whereas effects are characteristics that are a consequence of functions ("side" effects, not directly selected). Holmes (1986) points out that parasitic "... interactions should be important [in structuring helminth communities] only when species regularly co-occur at substantial population densities" (p. 203, brackets ours). We note, more specifically, that interactions based on adaptive responses (functions) of one parasite species to another cannot arise unless there is frequent co-occurrence over global gene pools.

We cannot imagine how the parasites under study here could have adapted to one another. Definitive hosts (fish and birds) are highly mobile and scatter parasite eggs widely and unevenly. Consequently, spatial distribution of these trematodes within and among host snail populations is patchy (Curtis and Hurd, 1983; Curtis and Hubbard, 1990), and there are abundant opportunities for trematode species to exist in isolation. The probability of co-occurrence generation after generation, particularly for specific parasites, is very low. Therefore, evolved parasite-parasite relationships are unlikely in this system. If interactions occur, they most likely result from effects, not functions. Our data indicating the lack of interactions among the majority of co-occurring trematodes, and the above considerations, justify eliminating models "c" and "d" (Fig. 1). Any evolved features of this system probably stem ultimately from the evolution of parasites to host, or possibly of host to parasites (models "a" and "b", Fig. 1).

In deciding between models "a" and "b", many of the same arguments apply. Gooch *et al.* (1972) found that

Ilyanassa obsoleta were electrophoretically homogeneous all along the eastern seaboard, pointing to extensive dispersal of larvae as the main cause. The planktonic larvae of *I. obsoleta* would then function analogously to parasite definitive hosts in the dispersal of progeny. Given the heterogeneity of trematode prevalence in *I. obsoleta* populations, many snail larvae would settle where parasites are not a frequent environmental challenge. If a snail were to obtain, by mutation, resistance to infection by one or more trematode species, its fitness probably would be enhanced in parasite-ridden environments such as parts of Cape Henlopen. Yet its progeny would very possibly settle where parasites are infrequent. The mutation, there, would be at best neutral. These considerations suggest that model "a" (Fig. 1) is the operative one—the only adaptive responses between species in the *I. obsoleta* system are most likely those of the parasites to the host.

The negative interaction between *Himasthla quissetensis* and *Lepocreadium setiferoides* in the *Ilyanassa obsoleta* system deserves comment because it seems to counter the proposition that these parasites are not adapted to each other. A lack of co-occurrence of these abundant species in *I. obsoleta* has been reported (Vernberg *et al.*, 1969; Curtis, 1985), but the detailed dissection methods used in this study revealed four co-occurrences (Table 1). Obviously, miracidia of both species reach the same host, and there is a subsequent eviction (apparently of *H. quissetensis*). This eviction is important in terms of determining composition of the infra- and component assemblages observed, but is it based on adaptation of one parasite to another? In keeping with the above reasoning—that parasite co-occurrence is not globally predictable enough to result in adaptations to other parasites—we interpret this negative co-occurrence as based on an effect rather than a function [an exaptation (Gould and Vbra, 1982)] because it results from the way these species have evolved to the host, not to each other. In ecological terms, such a phenomenon is a competitive exclusion. However, in our hypothesis, the exclusion occurs between two species that are adaptively unaware of each other. If species interactions are an evolutionary force driving the structuring of interactive, co-adapted species assemblages, then we should distinguish between function- and effect-based relationships among species. A deeper appreciation of causal relationships in ecological systems will require understanding these relationships.

Factors structuring the assemblage of larval trematodes in populations of the California estuarine snail *Cerithidea californica* have been examined by Sousa (1990) and Kuris (1990). Two direct lines of evidence convinced these authors that competitive exclusions were occurring among *C. californica* trematodes. Sousa (1990) cites personal laboratory observations in which dominant species preyed upon stages of subordinates. Both authors reported trem-

atode species replacements in individual snails periodically reexamined for infection by cercarial release. Kuris (1990) constructed a competitive hierarchy among trematode species in infracommunities, which he concluded would produce component community structure. In the *Ilyanassa obsoleta* system, such cercarial release data would have to be used judiciously because cercariae, even if present, often are not shed (Curtis and Hubbard, 1990). Data are not presented that assess this source of error for the *C. californica* system. In any event, there is considerable heterogeneity in prevalence of trematodes among *C. californica* populations (Kuris, 1990; Sousa, 1990). Parasite progeny are dispersed by definitive hosts similar to those in the *I. obsoleta* system, giving species the same opportunities to exist in isolation. This may mean that, whether they interact or not, parasites are not co-adapted in the *C. californica* system either. Because *C. californica* has direct development (Sousa, 1990)—making populations more insular—the host may have the ability to evolve to its parasites.

Several authors have examined snail-trematode systems for interactions among parasites infecting the same host individual. Some have emphasized direct microscopical observations of antagonisms occurring in freshwater snails (*e.g.*, Lie *et al.*, 1965; Basch *et al.*, 1969; Mouahid and Mone, 1990). Based upon such observations, there can be no doubt that antagonisms between trematodes can and do occur, but their frequencies in natural snail populations are less certain. Other authors have emphasized observations of multiple infections in marine (*e.g.*, Kuris, 1990; Sousa, 1990) and freshwater (*e.g.*, Fernandez and Esch, 1991a, b; Williams and Esch, 1991) gastropods. In no case are multispecies assemblages reported to be particularly frequent. Such species-rich assemblages are more frequent and various in the *Ilyanassa obsoleta* system on Cape Henlopen (Curtis, 1985, 1987, 1990; present study) than in any studied so far (see Cort *et al.* (1937)). The most frequent assemblage observed on Cape Henlopen is *Lepocreadium setiferoides* with *Gynaecotyla ahunca*, and it occurred in only 4.4% of snails ($n = 4870$) examined by dissection (Curtis, unpub. data). Individual occurrence of each was 16.9 and 20.3%, respectively. Thus, even when species can and do co-occur, the probability of co-occurrence is slight. The opportunity to evolve adaptive responses to other particular trematodes seems minimal or nonexistent, which suggests that models "c" and "d" (Fig. 1) may be generally inoperative. The best opportunity for trematode-trematode adaptive responses would be in a situation where all the necessary hosts are confined to one habitat, such as in a freshwater pond, as described by Williams and Esch (1991) and Fernandez and Esch (1991a). However, Williams and Esch (1991) and Fernandez and Esch (1991b) conclude that within-snail trematode interactions in their system are in-

frequent and not the factor structuring the infra- and component communities.

Can the host be adapted to its parasites? The evolution of a host to several parasites is a problem of "overwhelming complexity" (McLennan and Brooks, 1991), and the issue is not resolvable with the data at hand. Dobson and Merenlender (1991) suggest, as we content here, that the probability of such evolutionary responses would depend on host and parasite dispersal abilities. *Ilyanassa obsoleta*, because of its widespread dispersal, is unlikely to evolve to its parasites (model "b"), but it is a possibility with a snail in a more insular system, such as a pond.

How can the coexistence, in a small habitat unit, of several species with similar resource requirements be explained? This study has provided considerable comparative data on the fitness of parasites when they occur in different assemblages. The extensive variation in cercarial output (Table V) is not explainable by looking to presence or absence of other species. Perhaps resources for trematodes living in *Ilyanassa obsoleta* are somehow not limiting. We have suggested that the only adaptations (functions) in the system are those of the parasites enabling them to live in the snail (model "a", Fig. 1). We offer the following possible explanation. Each of these five trematodes has evolved to castrate the host snail. Castration of the host stems from a parasite adaptation to channel energy to the parasite that would otherwise go to the support of host gonadal tissue (Baudoin, 1975). *Ilyanassa obsoleta* is a long-lived host (7 years or more); the largest (oldest) snails are nearly all parasitized where trematodes are prevalent; and they appear not to lose infections (Curtis and Hurd, 1983). The host must survive the rigors of succeeding winters. A trematode adapted to such a host may have been selected to exact intermediate to minimal damage (besides castration) because it could then "farm" the host for many years (see Minchella *et al.* (1985) and Gill and Mock (1985) for similar interpretations of host-parasite systems). We propose that, if the trematodes of *I. obsoleta* operate this way, then they should not singly, or in multiples, drain resources to the extent that they become limiting. In brief, they can coexist if they are all adapted to live well below the level at which the host is stressed.

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